

# Predator traits determine food-web architecture across ecosystems

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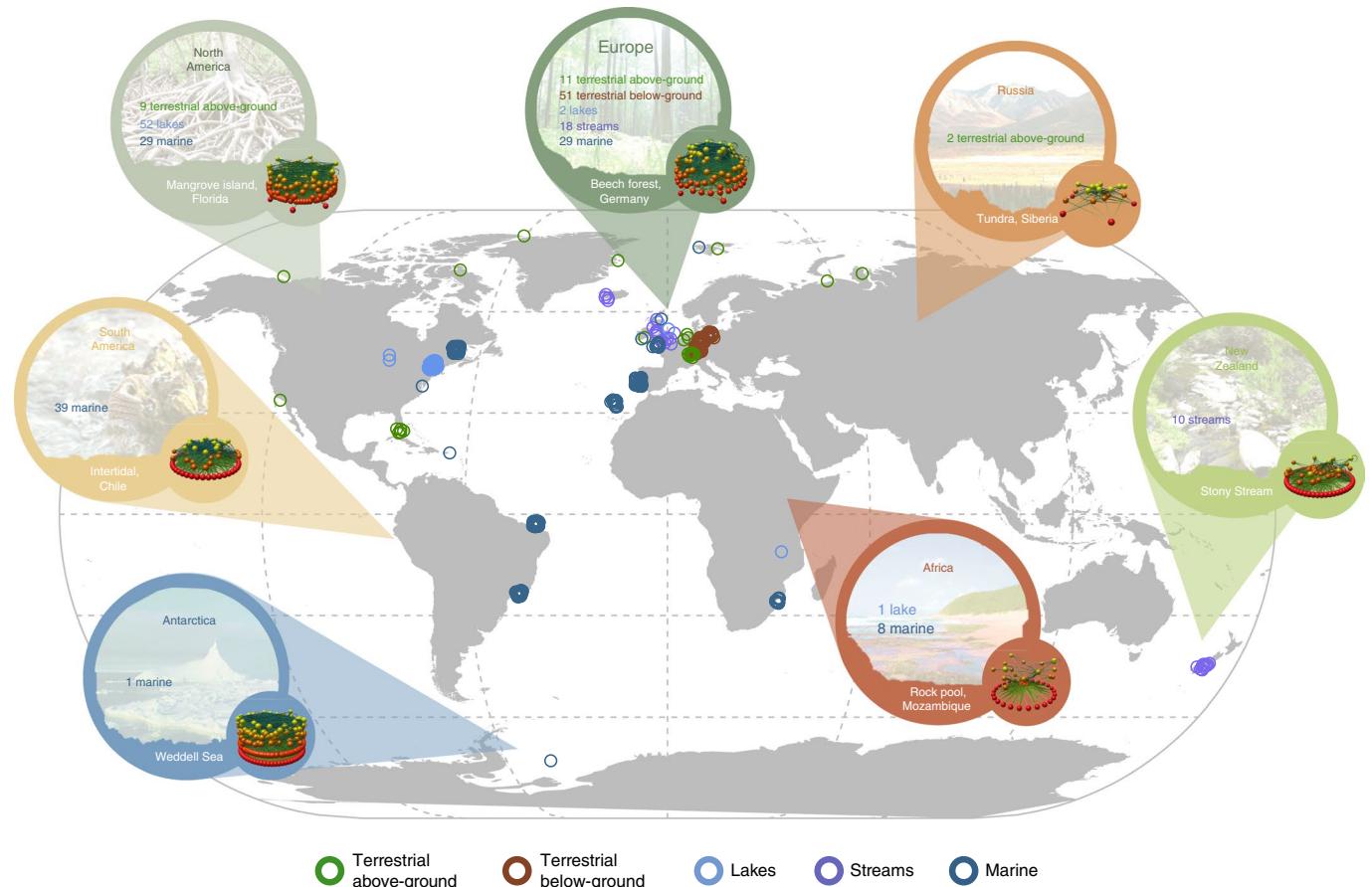
**P**redator-prey interactions in natural ecosystems generate complex food webs that have a simple universal body-size architecture where predators are systematically larger than their prey. Food-web theory shows that the highest predator-prey body-mass ratios found in natural food webs may be especially important because they create weak interactions with slow dynamics that stabilize communities against perturbations and maintain ecosystem functioning. Identifying these vital interactions in real communities typically requires arduous identification of interactions in complex food webs. Here, we overcome this obstacle by developing predator-trait models to predict average body-mass ratios based on a database comprising 290 food webs from freshwater, marine and terrestrial ecosystems across all continents. We analysed how species traits constrain body-size architecture by changing the slope of the predator-prey body-mass scaling. Across ecosystems, we found high body-mass ratios for predator groups with specific trait combinations including (1) small vertebrates and (2) large swimming or flying predators. Including the metabolic and movement types of predators increased the accuracy of predicting which species are engaged in high body-mass ratio interactions. We demonstrate that species traits explain striking patterns in the body-size architecture of natural food webs that underpin the stability and functioning of ecosystems, paving the way for community-level management of the most complex natural ecosystems.

Prey rarely, if ever, give up their lives willingly to their predators. Predators overcome their prey's resistance by being, on average, larger than their prey, yielding a systematic pattern in communities where the non-cannibalistic average ratio of predator-to-prey body mass (hereafter, body-mass ratio) is higher than unity<sup>1,2</sup>. Notable exceptions to this include when animals cooperate to overcome larger prey (for example, pack hunters) and where consumers are parasites or parasitoids. Variation in body-mass ratios within food webs typically spans several orders of magnitude and includes some predators that are smaller than their prey<sup>3</sup>, but is dominated by situations of the larger feeding on the smaller. The varying body-mass ratios limit which trophic interactions are realized in a community<sup>4–6</sup>, and the strength of these interactions<sup>7–9</sup>. Predators typically exert the strongest feeding pressure on prey that are 1–2 orders of magnitude smaller<sup>1</sup>, while weaker interaction strengths are realized with prey that are smaller or larger than this size<sup>10,11</sup>. Specifically, interactions of predators with small prey are characterized by high body-mass ratios that yield weak interactions with slow dynamics, which play a central role in maintaining food-web stability<sup>12–16</sup> and ecosystem functioning<sup>10,17,18</sup>. Moreover, they

also buffer natural communities against perturbations from global warming<sup>19</sup>, eutrophication<sup>20</sup> and secondary extinction waves<sup>21</sup>. Therefore, identifying these unique interactions is paramount to determining the stability of natural food webs to perturbations and functioning. However, applications of this concept to natural communities have been hampered by the difficulty of describing the myriads of interactions present in natural food webs. Using traits of predator species as proxies of body-mass ratios and the resulting interaction strengths that they govern could provide the means to understand which species are the drivers of community stability and functioning without having to perform the often logically and economically impossible task of quantifying entire interaction networks. This approach could ultimately help predict how extinctions, invasions and other anthropogenic environmental changes affect community stability and functioning through shifts in community trait structure.

Despite the importance of understanding how species traits affect body-mass ratios, there is much uncertainty about these relationships. A pioneering study<sup>22</sup> showed that vertebrate predators exhibit systematically higher body-mass ratios than invertebrates

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**Fig. 1 | Global distribution of food webs.** The global distribution of food webs in the GATEWAv database (v.1.0; see Supplementary information).

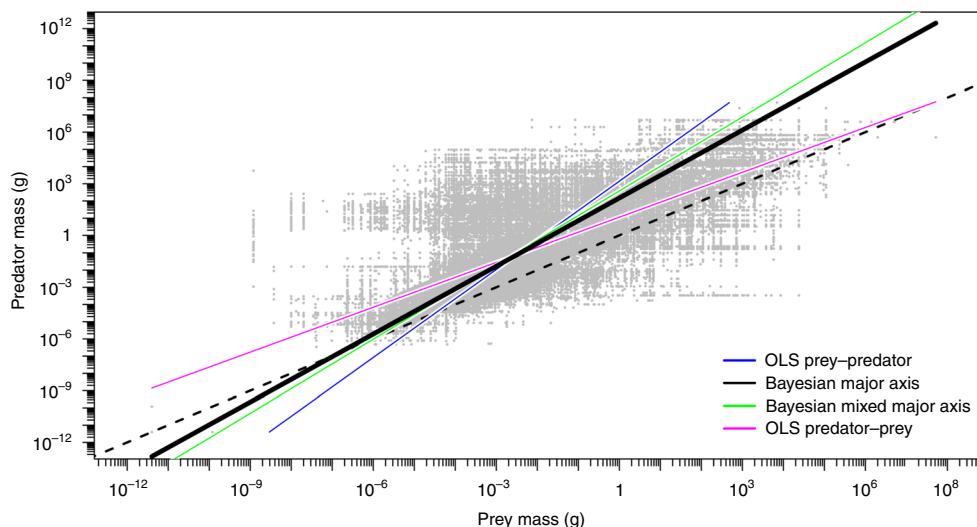
and this has been supported by subsequent analyses also documenting higher body-mass ratios in aquatic versus terrestrial communities<sup>1</sup>. These studies also found that predator–prey body-mass scaling is superlinear with slopes higher than unity, meaning that body-mass ratios increase with body mass (see Supplementary Fig. 1, red line). However, other studies have proposed that the scaling relationship is either sublinear (decreasing body-mass ratios with body mass; Supplementary Fig. 1, yellow line)<sup>2,22,23</sup> or superlinear<sup>1,2,23,24</sup>, depending on the ecosystem type<sup>2,23</sup>, predator metabolic group<sup>23–25</sup> or resource supply<sup>26</sup>. Additionally, besides body mass and metabolic type, little is known about how body-mass ratios vary with other species traits and across different ecosystem types. Predator and prey movement types and feeding behaviour are likely to influence scaling relationships by limiting maximum achievable attack speeds<sup>24,27</sup>. Interaction dimensionality, which describes whether predators forage in three dimensions (for example, the water column of lakes and oceans) or on two-dimensional (2D) surfaces (for example, epigaeal terrestrial or benthic aquatic predators), also influences predator–prey attack rates<sup>24,28</sup>. Since these variables affect the likelihood and strength of predator attack rates and scale with individual body mass, we expected that they should also modify the scaling relationship between predator and prey body masses.

Here, we provide a comprehensive assessment of how species traits modulate predator–prey body-mass scaling relationships and body-mass ratios in natural, complex food webs across an unprecedented range of ecosystems. To do so, we collated the most extensive global food-web database to date (GlobAl daTabasE of traits and food Web Architecture (GATEWAv) v.1.0), comprising 290 food webs (with 222,151 feeding links between 5,736 species; see Supplementary Table 1) distributed across the globe (Fig. 1), includ-

ing information on four different species traits and five ecosystem types (see Supplementary Table 2). First, we analysed the scaling of predator and prey body masses over 17 orders of magnitude (fresh masses ranging from the no. 2  $10^{-9}$  g protozoan *Bodo saltans*, to the no. 275  $10^6$  g sperm whale *Physeter macrocephalus*). Some prior studies advocated the use of major axis regressions to account for the bidirectional causality between predator and prey body mass<sup>1</sup>, whereas others used mixed-effects models to include the random effects of the study<sup>2</sup>. Since these two types of analyses are mutually exclusive in traditional statistics, we used Bayesian modelling to implement a combination of major axis regressions with mixed effects. Second, we tested for the importance of cofactors in this scaling relationship (ecosystem type, predator and prey metabolic types, interaction dimensionality, predator and prey movement types). These analyses address relationships between species traits and food-web architecture across ecosystems. Third, we developed predictions of average body-mass ratios of predators by their traits, which identifies ecological attributes that broadly predict ecological perturbation stability and functioning in natural communities without requiring detailed knowledge of complex food-web structure.

## Results

In our first analysis, we addressed the scaling of predator and prey body masses. Ordinary least-squares (OLS) regressions relating these two variables generate different slopes depending on which variable is chosen as the independent variable (Fig. 2, magenta and blue lines). This discrepancy arises because there is no unidirectional causal relationship between the two variables and because both have measurement errors of the same magnitude, which renders major axis regression the appropriate tool for analysing these data<sup>31</sup>. Thus,



**Fig. 2 | Overall scaling of predator and prey body mass assessed by four regression methods ( $n = 88,197$ ).** OLS regression of prey mass depending on predator mass (blue line), OLS regression of predator mass depending on prey mass (magenta line), Bayesian major axis regression (black line) and Bayesian mixed major axis regression with random intercepts (green line). Bayesian regression parameters are the means of the posterior distributions. The dashed line indicates equal body masses of predator and prey for comparison. All body masses are gram fresh masses. See Supplementary Table 3 for model parameters. Our extensive statistical considerations hold that the Bayesian major axis regression (black line) is the most appropriate model.

we used Bayesian modelling to fit a major axis regression, which makes no assumptions about a causal relationship between the variables. The major axis regression showed that the overall allometric scaling relationship between predator and prey body mass was superlinear, exhibiting a slope higher than unity (Fig. 2, black solid line; Bayesian major axis regression, slope = 1.315, 95% confidence interval: 1.307–1.323). This suggests that the body-mass ratios between predators and their prey increase with the masses of prey and predators (that is, the distance between the regression line and the dashed diagonal indicating equally sized predator–prey pairs). On average, interactions between relatively large predator and prey species are characterized by higher body-mass ratios than interactions between smaller species. The Bayesian approach also allowed us to fit mixed-effects models to the data, particularly the random effects on the intercept of the different studies (database variable, link.citation; see Supplementary Table GATEWAv metadata). This yielded a very similar scaling relationship as the non-mixed major axis regression (Fig. 2, green line). Based on the similarity of the results and statistical arguments (see Methods), we have based the following analyses on Bayesian major axis regressions, while the results of the analyses with Bayesian mixed-effects major axis regressions are shown in the Supplement.

In our second analysis, we used major axis regressions to fit six models of predator–prey body mass scaling that each contained one co-variable (ecosystem type, predator or prey metabolic type, predator or prey movement type, interaction dimensionality; see Supplementary Table 2 for variable description). Model comparisons demonstrated that adding any of these co-variables improves the fit substantially over the simple scaling model (Table 1, lower Watanabe–Akaike Information Criterion (WAIC) scores indicate higher model adequacy). According to these WAIC ranks, the best-performing models included predator metabolic type (rank 1) or predator movement type (rank 2) as co-variables, whereas models including the same trait variables of the prey led to lower ranks (Table 1, ranks 4 and 6). Hence, WAIC values suggested that predator traits were more important for determining body-mass scaling than prey traits.

While the overall relationship was superlinear (Fig. 3, black solid lines), the relationships for ectotherm and endotherm vertebrate predators exhibited strong sublinear scaling, implying that the

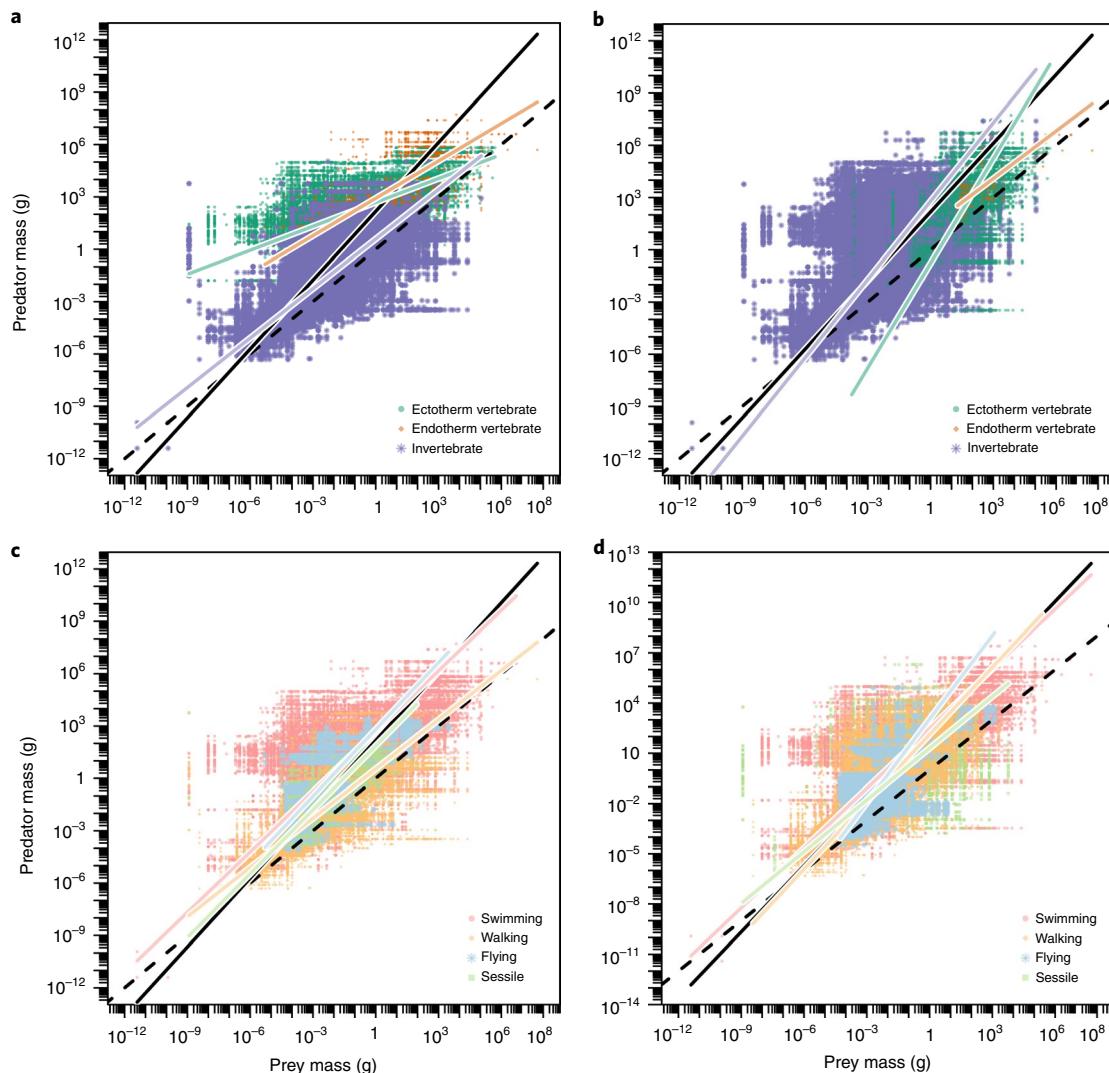
body-mass ratios of vertebrate predators decrease with their body mass (Fig. 3a). As vertebrate prey often have vertebrate predators, a similar pattern might be expected for the scaling relationship within the prey metabolic groups. Surprisingly, we found superlinear scaling for all vertebrate prey groups (Fig. 3b). Together, these results suggest that sublinear scaling characterizes vertebrate predators irrespective of whether their prey are vertebrate or invertebrate species.

The second most important co-variable in our analyses was predator movement type. Interestingly, we found that swimming, flying and sessile predators exhibit superlinear scaling relationships that are similar to the overall model, whereas walking predators exhibit sublinear scaling (Fig. 3c). Although many walking predators feed on walking prey, our analyses of the prey movement type show superlinear scaling across groups (Fig. 3d). Similar to the metabolic groups, this implies that changes in predator–prey body-mass ratios are mainly driven by predator movement type, irrespective of prey movement type. Together, our analyses of species' traits suggest that the traits of predators have stronger implications for scaling relationships and body-mass ratios than the traits of their prey.

Comparing the two environmental characteristics showed that ecosystem type (WAIC rank 3) improved the model substantially

**Table 1 | Comparison of six predator–prey body-mass scaling models with one co-variable; bayesian major axis models as in Figs. 3 and 4 and mixed Bayesian major axis models as in Supplementary Figs. 2–7**

Co-variable	Bayesian major axis model		Bayesian mixed major axis model	
	WAIC	Rank	WAIC	Rank
Predator metabolic group	$2.414 \times 10^5$	1	$2.229 \times 10^5$	1
Predator movement type	$2.720 \times 10^5$	2	$2.520 \times 10^5$	2
Ecosystem type	$2.722 \times 10^5$	3	$2.566 \times 10^5$	4
Prey metabolic group	$2.807 \times 10^5$	4	$2.563 \times 10^5$	3
Interaction dimensionality	$2.818 \times 10^5$	5	$2.616 \times 10^5$	6
Prey movement type	$2.830 \times 10^5$	6	$2.605 \times 10^5$	5
None	$2.859 \times 10^5$	7	$2.657 \times 10^5$	7

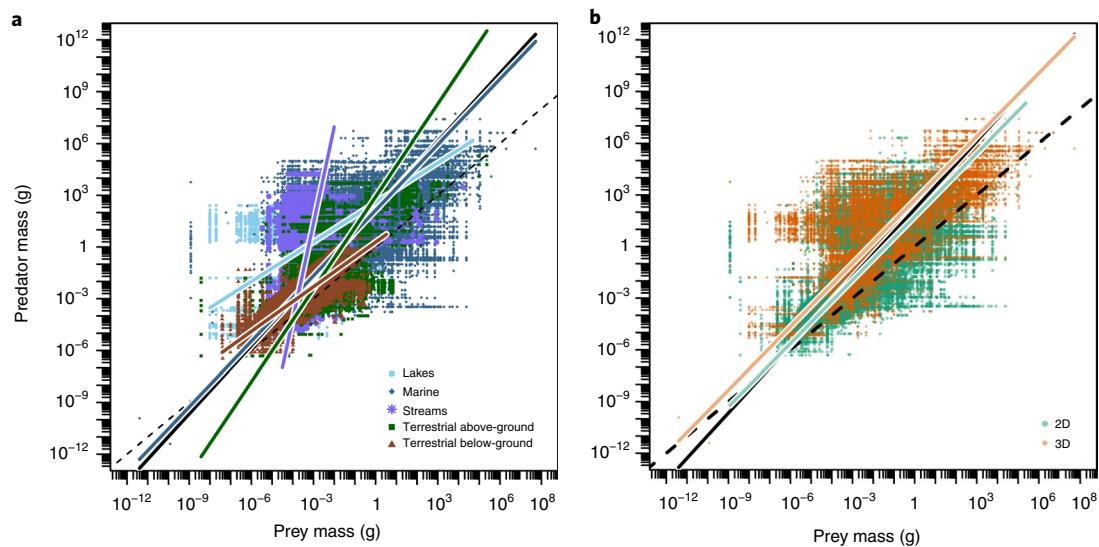


**Fig. 3 | Species' traits constrain the scaling of  $\log_{10}$  predator body mass with  $\log_{10}$  prey body mass ( $n = 88,197$ ). a, Predator metabolic type. b, Prey metabolic type. c, Predator movement type. d, Prey movement type. The solid black lines represent the overall scaling relationship; the coloured lines show the relationships for the subgroups. The Bayesian regression parameters are the means of the posterior distributions. The dashed lines indicate equal body masses of predator and prey for comparisons. See Supplementary Table 3 for model parameters.**

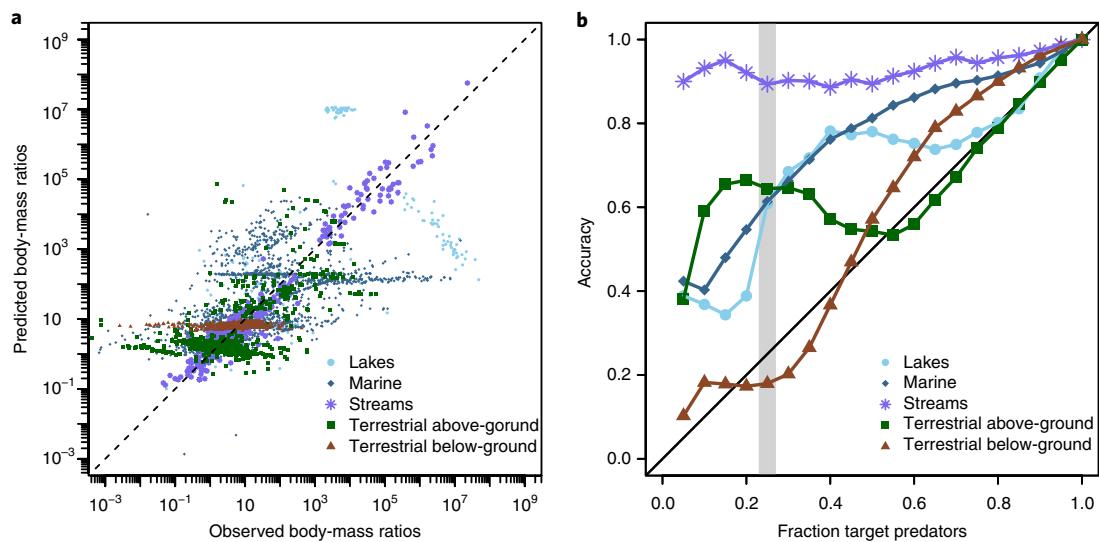
more than interaction dimensionality (2D versus three dimensional (3D); rank 5, Table 1). Among ecosystem types, marine, stream and terrestrial above-ground ecosystems follow superlinear scaling similar to the overall relationship (although streams followed steeper scaling relationships), whereas lake and terrestrial below-ground ecosystems exhibit sublinear scaling, parallel to each other (Fig. 4a). Both 2D and 3D interaction dimensionalities demonstrate superlinear scaling with a slope similar to the overall pattern. However, 3D interactions tend to involve predator-prey pairs with greater body-mass ratios compared to 2D interactions (Fig. 4b). Although many marine or lake interactions occur in the pelagic 3D part of the ecosystem, ecosystem type does not completely overlap with interaction dimensionality since these aquatic ecosystems also include benthic 2D interactions.

Finally, we addressed how well we can predict which predators in a food web have the highest average body-mass ratios compared with their prey in the absence of information on food-web structure and traits of the prey species. Thus, the statistical models included the predator traits (body mass, metabolic and movement type) and ecosystem type as independent variables ('predator-trait model'; see Methods for details and Supplementary Table 4 for parameters).

The overall predator-trait model fitted the data well (Fig. 5a). We found that predictive accuracy varied across ecosystem types and with the fraction of target predators (Fig. 5b). We anticipated that typically a low fraction of predators will be chosen for applied population management and used a fraction of target predators of 25% as an arbitrary example to illustrate our results (Fig. 5b, grey area; note that qualitatively similar results could be obtained for any fraction of 30% or lower). At this fraction of target predators, the accuracy of the predator-trait model predictions is almost always higher than the prediction accuracy when the same fraction of predators is chosen at random (Fig. 5b, diagonal line). An exception to this pattern were the terrestrial below-ground systems (Fig. 5b), potentially as a consequence of the substantially higher degree of omnivory in soil communities<sup>29</sup> or the widespread use of poison by soil predators<sup>32</sup>. In contrast, the predator-trait model had high accuracy in streams (89%), marine (61%), terrestrial above-ground (64%) and lake ecosystems (61%), exceeding the 25% accuracy of random predictions (Fig. 5b, diagonal line in the grey area). This implies that for these ecosystems the predator-trait model improves the predictions by a factor between 2.44 (marine and lake ecosystems) and 3.56 (streams), which is close to the maximum improvement factor



**Fig. 4 | Ecosystem characteristics constrain the scaling of  $\log_{10}$  predator body mass with  $\log_{10}$  prey body mass ( $n = 88,197$ ). a,** Ecosystem type. **b,** Interaction dimensionality. The solid black lines represent the overall scaling relationship; the coloured lines show the relationships for the subgroups. The Bayesian regression parameters are the means of the posterior distributions. The dashed lines indicate equal body masses of predator and prey for comparisons. See Supplementary Table 3 for model parameters.



**Fig. 5 | The predator-trait model predicts the target predators with the highest body-mass ratios across different ecosystem types ( $n = 7,296$ ). a,** Observed versus predicted average body-mass ratios characterize the goodness of fit ( $R^2 = 0.633$ , root mean square error = 0.914). The dashed diagonal line shows where observations and predictions are identical. **b,** Accuracy (proportion of correct predictions) in an out-of-sample food web depending on the fraction of target predators to be predicted. The diagonal line characterizes predictions when predators are chosen at random. The grey area corresponds to an exemplary fraction of 25% of predators with the highest body-mass ratios. See Supplementary Fig. 8 for variation in accuracy across the individual food webs.

of 4 (occurring with 100% prediction accuracy relative to the 25% random prediction accuracy at a fraction of target predators of 25%; grey shaded area in Fig. 5b).

## Discussion

Using a global database of 290 food webs, we show that (1) the overall allometric scaling relationship between predator and prey body mass is superlinear, implying that the largest species have the highest body-mass ratios and that (2) predator traits (metabolic and movement type) are more important than prey traits in determining these scaling relationships. Subsequently, we developed a predator-trait model that successfully predicted the predators with

the highest average body-mass ratio. Food-web theory has shown that these high body-mass ratios yield weak interactions with slow dynamics that are critically important for buffering communities against external perturbations and maintaining ecosystem functioning<sup>10,12–15,17,18</sup>. Historically, these theoretical results have had little real-world application because they require the logically challenging task of assessing all or at least a large fraction of the food-web links. By focusing on predator traits and ecosystem type while discarding prey traits and the specific links of the food webs, our predator-trait model provides a generalizable and feasible solution that can bridge the gap between food-web theory and applied ecosystem conservation. For instance, our results suggest that

population protection of small vertebrates (for example, mustelids) and large swimming (for example, sharks) or flying predators (for example, birds of prey) might be most effective at buffering natural communities against external perturbations such as extinctions, invasions, pollution, eutrophication and warming. This trait-based approach enables the management of perturbation vulnerability in natural communities without detailed knowledge of the food-web structure.

Within the debate over the allometric scaling relationships of predator and prey body masses in natural food webs, the superlinear relationship presented in this study is consistent with some prior studies<sup>1,2,23</sup>, while deviating from others that demonstrate sublinear scaling<sup>2,22,23</sup>. Our comparison of regression methods suggests that this discrepancy could be partially attributed to the alternative use of major axis regressions<sup>1</sup> (consistently yielding superlinear scaling) or OLS regressions<sup>2,22,23</sup> (suggesting superlinear or sublinear scaling depending on which is the independent variable). Our comparison of the two OLS regressions with either predator or prey mass as the independent variable reveals substantial uncertainty since they make opposite predictions on how body-mass ratios scale with predator and prey mass, and there is no a priori argument over which OLS regression should be preferred. Hence, major axis regressions are the most appropriate statistical method because (1) there is no a priori expectation for a causal relationship between predator and prey mass and (2) both body masses are quantified with the same measurement error<sup>31</sup>. Our results show that major axis regression is not only statistically more appropriate but also that the choice of statistical approach has important implications for the biological interpretation of the allometric scaling relationship. This approach, combined with our newly compiled food-web database, has allowed us to refine our understanding of how the scaling relationship between predator and prey body mass varies across ecosystems and between predator–prey combinations of different movement type and metabolic group.

Despite the overall superlinear relationship between predator and prey body mass, our analyses identified several species' traits and ecosystem characteristics that are associated with a sublinear scaling relationship. Most notably, both ectotherm and endotherm vertebrate predators demonstrate strong sublinear scaling, making predator metabolic type the most important factor among those we considered for predicting predator–prey body-mass scaling relationships. Consistent with previous research<sup>1,22,23</sup>, we found that large vertebrate predators tend, on average, to feed on prey that are more equally sized (for example, orcas feeding on minke whales), whereas small vertebrate predators consume relatively smaller prey (for example, arctic foxes preying on lemmings). This result suggests that large and small vertebrate predators may be constrained by different factors, such as the limitations of maximum attack speed which are only experienced by the largest species<sup>27</sup>. Interestingly, some (often large) vertebrate predators hunt in groups to attack larger prey to improve their attacking success and overcome the body mass and speed constraints. Indeed, the next most important factor in our analysis was predator movement type, which separates species categories of different speeds (for example, flying predators are faster than walking predators). In our analysis, walking predators demonstrate sublinear scaling in contrast to all other movement types. The highest body-mass ratios were observed for the largest swimming and flying predators. Further investigations of the physiological constraints related to predator movement type, metabolic type and relative predator–prey body masses on predator feeding rates would help illuminate the processes behind these observed patterns.

Generally, our model selection results suggest that predator metabolic and movement traits had much stronger effects on the scaling relationship than the equivalent prey traits. This is partially supported by the greater similarity between the major axis regression

(accounting for bidirectional causalities) and the OLS regression with prey body mass as the dependent variable. Therefore, we conclude that top-down prey selection by predators has a stronger effect on prey mass than does the bottom-up influence of prey mass on predator mass. It is likely that both top-down and bottom-up influences are important, but our results indicate the dominance of the former, which stimulated the development of the predator-trait models of our third analyses predicting which predators have the highest average body-mass ratios across food webs.

Our results also identify ecosystem type as an important cofactor of the predator–prey body-mass scaling relationship, which is generally consistent with prior studies<sup>23,24,33</sup>. We expected this effect to be partially explained by the habitat dimensionality of the interaction (2D or 3D), which has important consequences for the strength of predator attack rates<sup>24,28</sup>. Although we found an effect of interaction dimensionality with overall higher body-mass ratios in 3D than in 2D habitats, surprisingly it did not explain the different scaling relationships between different ecosystem types. This may be explained by the fact that the ecosystem type varies across food webs, whereas variance in interaction dimensionality plays an important role across the different predator–prey pairs within food webs. The superior explanatory power of the model including ecosystem type compared to that including interaction habitat dimensionality suggests that there are ecosystem characteristics not related to dimensionality, such as laminar viscosity, that may have a stronger effect on predator–prey interactions. We found relatively high body-mass ratios and a very steep body-mass scaling relationship in stream ecosystems. Streams exhibit several differences to the other ecosystem types of our database: (1) the higher physical drag force of the water; (2) the higher dependence on allochthonous resources; (3) the dendritic environmental structure; and (4) the relatively narrower range of body masses included in our data. While each of these points could be responsible for the difference in scaling relationships, the last point calls for additional data on stream interactions between larger species such as fish to see if the steep increase in the scaling relationship holds. While terrestrial above-ground and marine interactions exhibited superlinear scaling relationships as the overall relationship, those of lake and terrestrial below-ground systems were sublinear. Furthermore, the lack of vertebrate predators with high body masses and high body-mass ratios may at least partially explain this for soil communities; however, this surprising result requires more mechanistic investigation of the so far untested similarity between lake and below-ground interactions.

Our approach to characterize predator–prey body-mass ratios in natural food webs has some limitations. First, to encompass a wide range of body masses, taxonomy and ecosystem types, we assumed that interacting individuals have population-averaged body masses<sup>34</sup>. As in prior studies<sup>1,22,23,33</sup>, we relied on population-averaged body masses, since we rarely have measurements for the actual body masses of the interacting individuals. Thus, for many predator species, particularly those with ontogenetic diet shifts, actual body-mass ratios are likely to have a lower variation than body-mass ratios calculated from population averages. Unfortunately, the lack of individual data for entire food webs across ecosystems hampers any alternative approach. As prior comparisons of individual-based versus population-based food webs have shown<sup>34,35</sup>, our population-based approach probably underestimates the intercepts of the scaling relationships. Second, the study sampling design, environmental factors such as temperature and species' phylogeny may also affect the scaling relationship<sup>25,36–38</sup>, and these would ideally be included as co-variables in the analyses. Since these data were not systematically available for the data sets included, we accounted for them by random effects in mixed models<sup>2</sup>, which leaves the need for more detailed analyses for future studies. As major axis regressions with random effects are not generally available, we addressed this issue by using Bayesian models throughout the study, which

allowed comparisons with hierarchical models including random effects (that is, mixed-effects models). Although the mixed-effects model results do not change our findings substantially (see the Supplementary information for a comparison between mixed and non-mixed Bayesian models) and, due to potentially confounding clustering effects (see Methods), we have focused our analysis on the model without mixed effects. Third, our analyses were restricted to predator–prey interactions, whereas interactions of other consumer types such as parasites, parasitoids or herbivores were excluded. Since these interaction types are typically characterized by different body-mass ratios<sup>1,39,40</sup>, future studies should address their scaling relationships in our GATEWAY database. Fourth, we employed simple scaling relationships with up to one single co-variable to gain an in-depth mechanistic understanding, whereas models with interactions between multiple co-variables were omitted from our analyses of the predator–prey body-mass scaling. However, these more complex relationships with higher-order interactive effects could be addressed using black box approaches such as machine learning algorithms, which could provide accurate predictions of food-web structures<sup>32</sup>. Fifth, our study illustrates systematic differences in body-mass ratios across ecosystem types and species' traits, whereas explanations for these differences remain to be revealed by studies integrating mechanistic models with our data.

Our analyses provide insights into how predator and prey body masses scale with each other in natural food webs. The discovery that predator traits are more important than prey traits in predicting body-mass scaling and that ecosystem type has a greater effect than interaction dimensionality offers new possibilities for understanding and predicting differences in food-web structure, community stability and ecosystem functioning across community and ecosystem types. Specifically, our results highlight that critically important high body-mass ratios occur in interactions with predators that are (1) small vertebrates or (2) large swimming or flying species. With only three species traits (body mass, metabolic and movement type), our models could predict which 25% of the predators possess the highest average body-mass ratios with surprisingly high accuracy in most ecosystem types (58–89%). We anticipate that this accuracy will be increased by additional species traits (for example, predation strategy, use of poison, sub-habitat association) that compose the multiple dimensions of natural food webs<sup>6,32</sup>. Our trait-based food-web analyses enable generalizations of food-web theory from the food webs studied to the vast majority of communities for which only species and trait information is available. Updated with additional traits, this approach has great potential for managing ecosystem functioning and stability against external perturbations such as pollution, eutrophication and warming without full knowledge of food-web structure. Therefore, the trait-based body-mass ratio approach presents an important integration of food-web theory with applied ecosystem management that provides a theoretical foundation for the community-level conservation of the most complex natural ecosystems.

## Methods

We compiled a global database of traits and food-web architecture (GATEWAY v.1.0; see Supplement), where each link is characterized by the taxonomy and trait variables of both the consumer and the resource (see Supplementary Metadata for the variables). We included food webs with: (1) a sufficient quality in terms of taxonomic resolution, which prevents nodes aggregating species with very different trophic interactions; (2) a reasonable completeness integrating all trophic levels and community compartments; (3) trait information for the trophic species including at least their population-averaged body mass, their metabolic type and their movement type (see Supplementary Metadata for definitions); (4) information for each trophic link such as the type (for example, predatory), the dimensionality (2D and 3D) and the classification (individual-based and non-individual-based) (see Supplementary Metadata for definitions); (5) descriptors for the ecosystems such as ecosystem type and geographic location.

In our analyses, we focused on predatory (variable, interaction.type) and individual-based (variable, interaction.classification) interactions. The former

excludes interactions of other types (for example, herbivorous, detritivorous, parasitic, parasitoid), whereas the latter discards interactions of consumers attacking groups, swarms or films of resources (for example, filter feeding, grazing). Some of the studies included in our database sampled the same ecosystem at different locations, resulting in replicated predator–prey species pairs<sup>29</sup>. To avoid pseudoreplication, each unique combination of taxonomy, life stage and individual body mass for predator and prey species was included only once. After exclusion of interactions with missing variables, the resulting data included 88,197 unique predator–prey interactions among the original 222,151 feeding links.

First, we analysed the reduced data for the relationship between the  $\log_{10}$  of predator and prey body masses (gram fresh mass). We compared the fit of two OLS regressions (either predator mass or prey mass as the dependent variable) to that of a major axis regression and a mixed-effects major axis regression including random effects on the intercept of the different studies (variable, link.citation). Traditional methods only allow to fit either major axis regressions or mixed models with random effects. Hence, our aim of comparing major axis regressions with and without random effects (that is, random intercepts for each study) could only be achieved by realizing models that were fitted by Bayesian methods using the RStan package<sup>30</sup> (see Supplementary Statistical Methods for details). Consistent with traditional major axis regressions, we minimized the sum of squared orthogonal distances of the observations ( $x, y$ ) to the regression line<sup>31</sup> instead of the vertical distance ( $y$ ) as in OLS (model I) regressions.

Second, we used Bayesian major axis models to compare the fit of the simple scaling model to six models, whereby each included one co-variable: ecosystem type; predator or prey metabolic type; predator or prey movement type; or interaction dimensionality (see Supplementary Table 2 for variables). Overall, the results were mostly consistent between the mixed-effects and non-mixed models. The mixed-effects models fitted the relationships separately for each study. As the body-mass ranges within studies do not cover the entire body-mass gradient and the number of data points within studies is much lower than in the entire database, some of the fitted scaling relationships can become arbitrary as single points can strongly affect the slope. Averaging across all slopes and all intercepts using hierarchical approaches can lead to clusters of such arbitrary slopes, which can exert substantial leverage on the average relationship across all studies. In our data, the clustering remained even when using random intercepts and a fixed slope across all studies. Therefore, mixed-effects modelling of our data suffered from two limitations: (1) it loses information about the overall trend across the whole database (that is, none of the study-specific scaling relationships spans the entire body-mass gradient); and (2) the joint mean slope and intercept are affected by partially arbitrary slopes (data sets with few points). Since both regressions also yielded qualitatively similar results, we report the results of the non-mixed major axis regressions in the article (Figs. 3 and 4) with comparisons to the fits of the mixed major axis regressions in the Supplementary information (Supplementary Figs. 2–7). Model comparison (based on their WAIC values) of these seven models (the simple model without co-variable and the six models with one co-variable each) provided a ranking of their performance; we used the model parameters to gain an understanding of how they modify the relationship. In the analysis of predator–prey body-mass scaling, we refrained from analysing more complex models with interactions between these co-variables for three reasons: (1) they imply impossible combinations (for example, swimming predators in terrestrial ecosystems); (2) their higher-order interactions hamper the mechanistic understanding of individual effects; and (3) their strong collinearity causes interference between factors.

Third, we analysed our database for the dependence of the predators' average predator–prey body-mass ratios on predator traits (body mass, metabolic and movement type) and ecosystem type. To avoid circularity in the statistical model (predator body mass in both the dependent and independent variables), we fitted Bayesian major axis regressions with  $\log_{10}$  prey mass as the dependent and  $\log_{10}$  predator mass as the independent variables with the co-variables predator metabolic type, predator movement type and ecosystem type. We restructured the resulting predator-trait model equation to calculate the effect of the independent and co-variables on predator–prey body-mass ratios. By discarding prey species traits, these analyses allow prediction of which predators in a community have the highest average body-mass ratios without knowledge of the predator–prey links.

The accuracy of this approach was determined in a five-step cross-validation process. First, we chose one of the food webs ('test data') and ranked its predators according to their empirical average body-mass ratios. Second, we ran the predator-trait regression model described earlier in the remaining database containing the other 289 food webs ('training data') to predict the predators' average body-mass ratios depending on their traits. Third, we calculated the proportion of predators that were correctly predicted by this predator-trait model (hereafter: accuracy) for a fraction  $x$  of the highest ranked predators of the test data food web (hereafter: fraction of target predators). For example, a fraction of target predators of 0.1 implies that the 10% highest ranked predators (that is, those with the highest average body-mass ratios) of the empirical test data are compared to the 10% highest ranked predators as predicted by the predator-trait model of the training data. An exemplary accuracy of 0.8 would indicate an 80% overlap between the two species lists. Fourth, this assessment of prediction accuracy was systematically replicated across a gradient in the fraction of target predators  $x$ .

between 5 and 95% (steps of 5%). Finally, these four steps were repeated for each of the 290 food webs independently to calculate the average accuracy across food webs depending on the fraction of target predators.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

The data supporting the findings of this study (GATEW<sub>A</sub> 1.0) are available at the iDiv data repository<sup>41</sup>.

## Code availability

The R code of the statistical analyses is available as a Supplement.

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## Author contributions

U.B. developed the study design. U.B., P.A., A.D.B., L.-F.B., T.B., J.C.-C., E.C., M.D., C.D., A.D., A.A.V.F., K.F., B.G., C.G., J.H., M.R.H., U.J., M.J., S.K., O.M., M.M.M., E.L., K.L.-D., P.L., Y.L., C.M., N.D.M., V.M., C.M., S.A.N., E.J.O., D.O., J.P., D. Perkins, D. Piechnik, I.P., D.R., B.C.R., B.R., R.R., A.S., E.H.S., N.S., M.S.A.T., R.M.T., F.V., C.V., S.W., J.M.W., R.J.W., E.W., G.W. and A.C.I. gathered, contributed or organized data. U.B. and B.R. carried out statistical analyses. M.R.H. created the figures. U.B. and A.C.I. wrote the first draft of the manuscript. All authors discussed the results and commented on the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

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Study description	Metastudy across 290 natural food webs.
Research sample	All consumer-resource links of the 290 food webs were included.
Sampling strategy	With n=88,197 the sample size was more than adequate for all analyses.
Data collection	The data were collected by the primary authors and added to the database in collaboration with the first author.
Timing and spatial scale	NA
Data exclusions	NA
Reproducibility	All data and the R code are publically available.
Randomization	NA
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